植物研究雜誌
J. Jpn. Bot.
82: 137–144 (2007)

Reproductive Structures and Seasonality of *Dictyopteris latiuscula* (Dictyotales, Phaeophyceae) from the Pacific Coast of Japan

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(Received on January 5, 2007)

Reproductive structures of *Dictyopteris latiuscula* from the Pacific coast of Kanto, Japan and reproductive seasonality in Shimoda, Shizuoka Pref. were studied. This is the first report of female gametophytes and oogonia of the species. Mature sporophytes and gametophytes were simultaneously collected in late spring to early summer. Reproductive season of the species was differed between Chiba and Shizuoka.

Key words: *Dictyopteris latiuscula*, Dictyotales, Phaeophyceae, reproductive structure, reproductive seasonality.

Dictyopteris is a peculiar taxon among Dictyotalean seaweeds for their thallus structure with a blade consisting of a midrib running the center of a blade and wings both sides of it. About 40 species of the genus are described so far. The species of *Dictyopteris* show isomorphic alternation of generations by sporophytes and dioecious gametophytes. Three types of reproductive organs are produced; tetrasporangia on sporophytes, oogonia on female gametophytes and antheridia on male gametophytes. Several patterns of the characters of formation and arrangement of reproductive organs have been suggested (Phillips 1998, 2000, Hasegawa and Tanaka 2000)

Dictyopteris latiuscula (Okamura) Okamura (Dictyotales, Phaeophyceae) is endemic to Japan and the adjacent regions. Okamura (1902) described this species as *Halyseris latiuscula* based on materials from the Pacific coast of Japan. Later, he showed the morphology of the species including sporangia with several illustrations (Okamura 1907). Kawai (2001) showed sporangia and antheridia on material from the Seto Inland Sea. Few detailed observations have been made on the species, and this may be attributable to the difficulty in collection from their deep habitat (ca. 22 m; Okamura 1936). Female gametophyte and oogonia have never been reported. The reproductive seasonality and life history of the species in nature are not well known, though Okamura (1907) described that the sporangia are produced in spring.

We found sporophytes and female and male gametophytes of *Dictyopteris latiuscula* on the Pacific coast of Honshu, Japan. This study attempted to describe the detailed morphology of reproductive organs of *D. latiuscula*, and to clarify the specific features of the reproductive structures of the species by comparison with the other species of *Dictyopteris*. Furthermore the reproductive seasonality was inferred from collected plants.

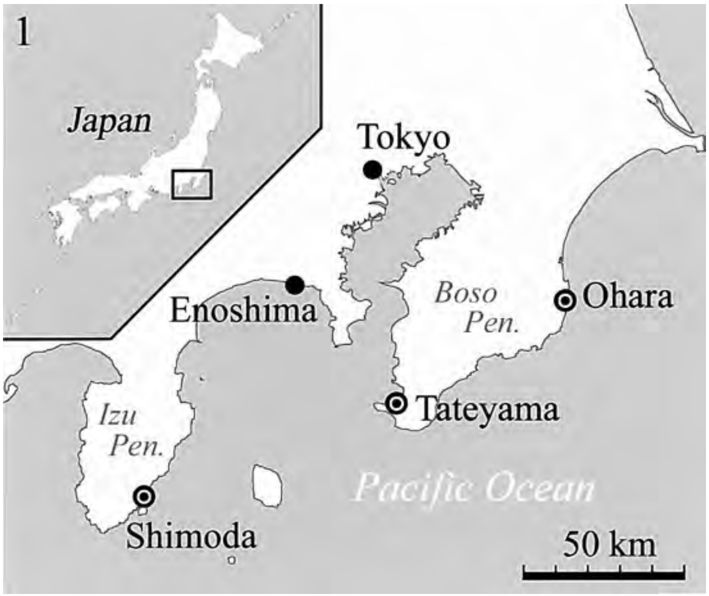


Fig. 1. Map of collecting sites (indicated with double circles).

Materials and Methods

Plants were collected from three sites of the Kanto district, Pacific coast of Honshu, Japan from 1998 to 2001 (Fig. 1, Table 1). Materials were picked out from among various seaweeds washed ashore. They were immediately fixed in 10 % formalin seawater solution after collection, to prevent rapid withering, and carried back to the laboratory. Semi permanent microscopic slides were made from liquid preserved specimens and mounted with a 2:3 mixture of water and corn sugar syrup with a little formalin. Sections for anatomical observations were prepared with a freezing microtome (Yamato Kohki Industrial Co., Asaka) and stained with 1 % aqueous aniline blue solution as the need arose. Differential interference contrast (DIC) optics (Nomarski apparatus, Nikon) were used for some photographs. Specimens examined have been deposited in the Museum of Tokyo University of Marine Science and Technology (MTUF-AL). Observations of reproductive organs were made on the fully matured plants. The cell sizes are given as follows: [minimum]-[maximum] ([average] ± [SD]). The sizes of reproductive organs are measured on the materials from Shimoda.

For checking the reproductive seasonality of *D. latiuscula*, collections were carried out at Shirahama, Shimoda City, Shizuoka Pref. almost twice a month from April 2000 to April 2001 (Apr. 4, 22; May 3, 22; Jun. 7, 20; Jul. 3, 17; Aug. 1, 30; Sep. 14, 28; Oct. 13, 28; Nov. 14, 28; Dec. 13, 28 in 2000 and Jan. 24; Feb. 9, 23; Mar. 9; Apr. 11 in 2001).

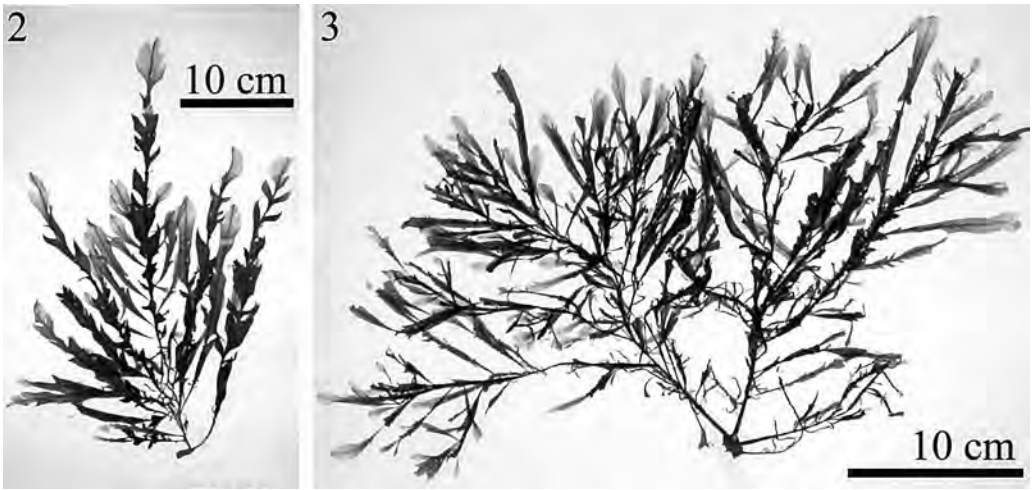
Results

Dictyopteris latiuscula (Okamura) Okamura in Rec. Oceanogr. Works Jpn. **4**: 75. (1932) – Segawa, Col. Illust. Seaweeds Jpn. 28, pl. 15, no. 126. (1956) – Chihara, Seaweeds Jpn. 56 (1983) – Yoshida, Marine algae Jpn. 207, pl. 2–6C (1998) – Kawai, Kôbe no Kaisô 69 (2001).

Halyseris (≡ *Haliseris*) *latiuscula* Okamura, Nippon Sourui Meii 111 (1902); Icon. Jpn. alg. **1**: 59, pl. 14, f 1–4 (1907) – *Neurocarpus latiuscula* (Okamura) Oka-

Table 1. Collection site and date of *Dictyopteris latiuscula*

Collection site	Date	Specimen number of MTUF-AL	Generation/Sex
Shimoda, Shizuoka Pref.	June 28, 1999	F 691–696, 698, 709, 711	sporophyte
(34º41´N 138º58´E)	July 3, 1999	F 697, 708	female
		F 699, 710	male
		F 712–714	sporophyte
		F 715	male
Tateyama, Chiba Pref.	May 17, 1999	F 633	immature
(34º59´N 139º49´E)	May 18, 1999	F 635–637	sporophyte
		F 649, 652	sporophyte
		F 648	female
Ohara, Chiba Pref.	May 15, 1999	F 630	sporophyte
(35º14´N 140º24´E)		F 631	female



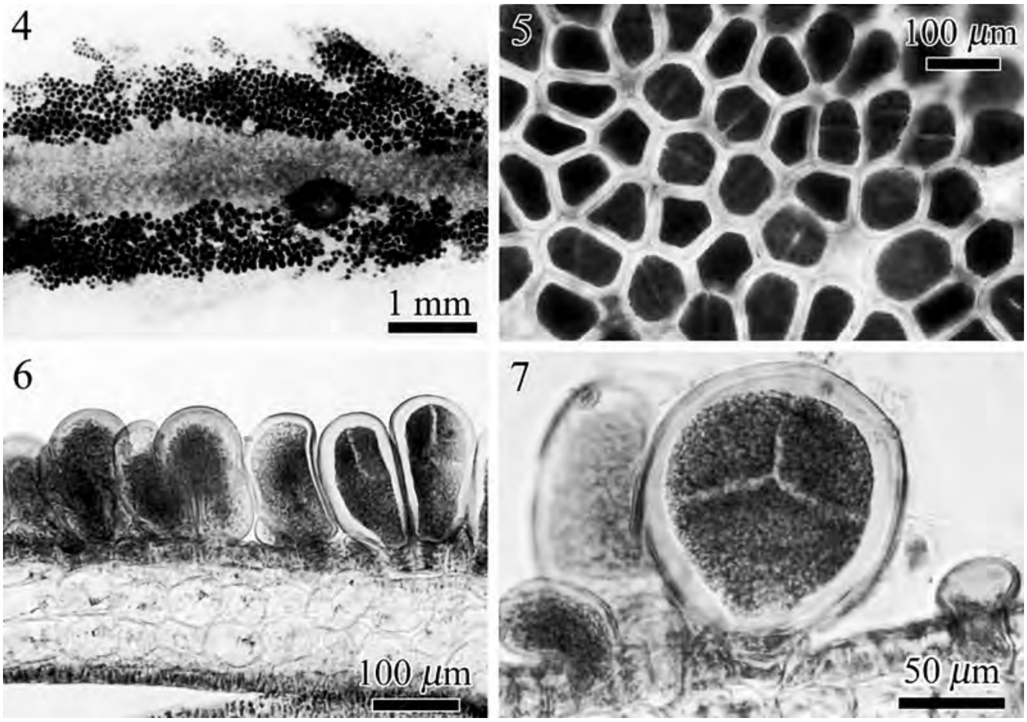
Figs. 2–3. *Dictyopteris latiuscula*. Fig. 2. Young thallus (MTUF-AL-20774, April 22, 2000, Shirahama, Shimoda City, Shizuoka Pref.). Fig. 3. Mature thallus (MTUF-AL-20773, June 28, 1999, Shirahama, Shimoda City, Shizuoka Pref.).

mura, Nippon Kaisô-shi 174 (1936).

Japanese name: Yahazu-gusa.

Representative specimens examined: JAPAN: Ohara, Chiba Pref. (K. Hasegawa, May 15, 1999, MTUF-AL-F 630, sporophyte; MTUF-AL-F 631, female); Tateyama, Chiba Pref. (K. Hasegawa, May 17, 1999, MTUF-AL-F 633, immature; MTUF-AL-F 635–637, sporophyte; K. Hasegawa, May 18, 1999, MTUF-AL-F 649, 652, sporophyte; MTUF-AL-F 648, female); Shimoda, Shizuoka Pref. (K. Hasegawa, June 28, 1999, MTUF-AL-F 691–696, 698, 709, 711, sporophyte; MTUF-AL-20773, immature; MTUF-AL-F 697, 708, female; MTUF-AL-F 699, 710, male); K. Hasegawa, July 3, 1999, MTUF-AL-F 712–714, sporophyte; MTUF-AL-F 715, male; K. Hasegawa, April 22, MTUF-AL-20774, immature).

A thallus (Figs. 2, 3) is composed of a holdfast and blades that consist of a midrib and wings at both sides. Branching mainly occurs by proliferation, and dichotomy seldom occurs. New blades are grown ascendingly from each side of the midrib flank. Proliferous branching successively

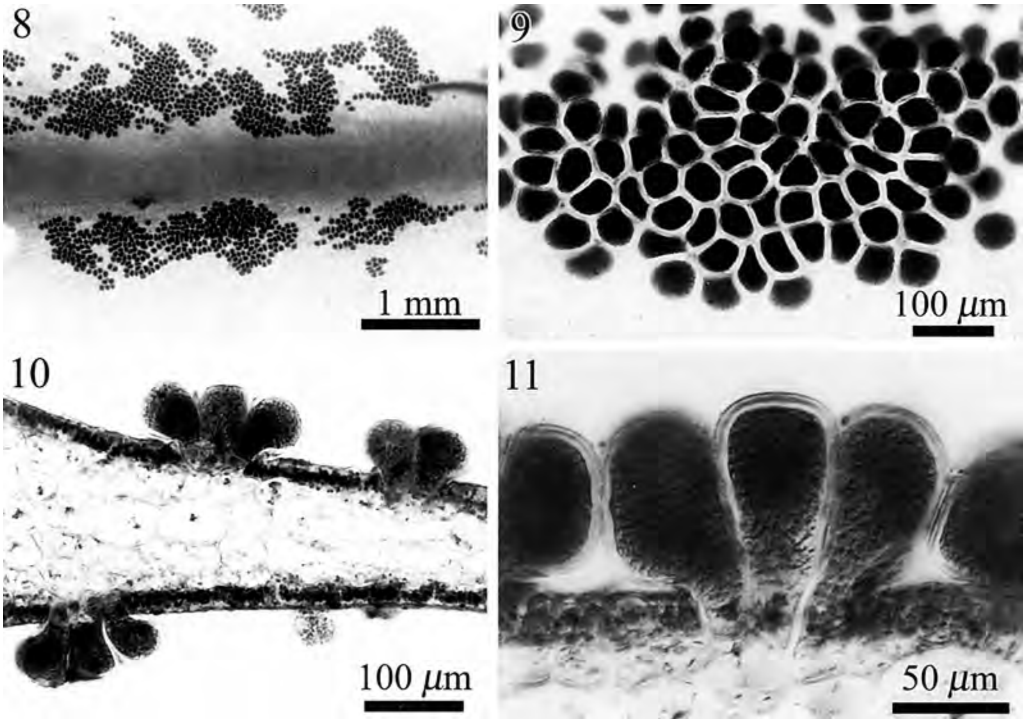


Figs. 4–7. Sporangia of *Dictyopteris latiuscula*. Fig. 4. Surface view of a sporophyte. Sporangial sori are seen on both sides of a midrib. Fig. 5. Surface view of sporangia. Sporangia containing tetrad are seen. Fig. 6. Transverse section (TS) of sporangial sorus. Sporangia completely project above the cortex and tightly aggregate. Fig. 7. Fully matured sporangium (TS).

occurs up to eight times in a mature thallus. Young immature individuals have a small number of broad blades with wings, and attain 28 mm wide (Fig. 2). Mature thalli producing reproductive organs attain 30 to 50 cm length and grow many small and narrow blades (attain 15 mm wide) (Fig. 3). All of reproductive organs are formed on the wings of these small blades. Most of the old blades lose wings and become stem-like. The holdfast is conical in shape and consists of complicated brownish filamentous rhizoids grown from cortical cells. The midrib adjoining the holdfast grows short rhizoids.

A blade is composed of a medulla and cortex in transverse section. The medulla consists of 12 to 20 layers of cylindrical cells in the midrib and 2 to 3 layers of compressed cells in wings. The cells of the midrib are arranged parallel to the long axis of the blade, while those of the wings are obliquely arranged to the midrib. The cortical cells are elongated in the midrib, while in the wings, those are shorter and wider than in the midrib. All kinds of reproductive organs originate from the cortical cells of wings.

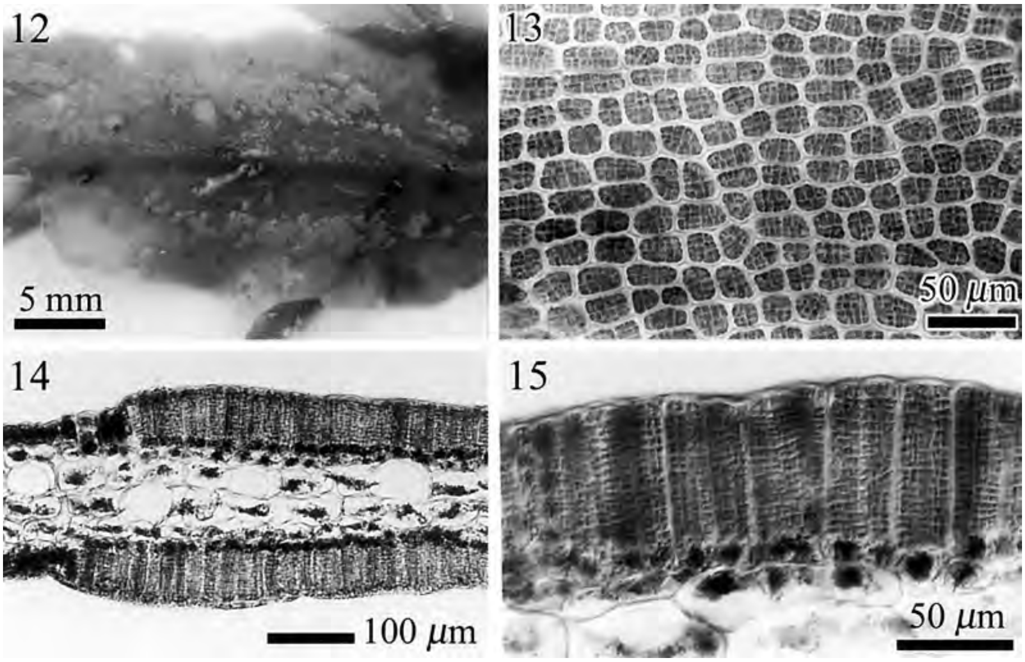
In blades of 5 to 20 mm wide from Tateyama, the cortical cells of the midrib were 20–60 (35 ± 9) μm in length and 11–30 (19 ± 4) μm in width, and that of mid-part of wings are 17–47 (28 ± 6) μm × 12–33 (20 ± 4) μm, in surface view. In blades of 8 to 12 mm wide from Shimoda, the cortical cells of the midrib were 15–50 (29 ± 7) μm × 6–22 (14 ± 3) μm, and that of wings were 17–44 (26 ± 5) μm × 10–31 (18 ± 4) μm. The sizes of cortical cells are significantly different between specimens from the two sites.



Figs. 8–11. Oogonia of *Dictyopteris latiuscula*. Fig. 8. Surface view of a female gametophyte. Oogonial sori are formed on both sides of the midrib. Fig. 9. Surface view of an oogonial sorus. Oogonia at the same developmental stage are clustered together. Fig. 10. Oogonial sori (TS) formed both surfaces of the blade. Fig. 11. Oogonia (TS) completely project above cortex with a stalk cell.

Structure of sporangium Sporangial sori are recognized as dark brownish lines or small spots along the midrib (Fig. 4). As maturation progresses, the sori grow broader by formation of new sori nearby. A developed sorus attains 3 mm wide, extends from the base to near the tip of a blade and consists of sporangia at various stages (growing, containing tetrads, after spore release) (Figs. 5, 6). The development of sporangia begins by turning dark brown and outward swelling of cortical cells. Developed sporangia, which are spherical to elliptical in shape, produce several stalk cells below and project above cortex (Figs. 6, 7). A fully matured sporangium, which contains tetrads, is 80–144 (121 ± 12) μm across and 120–164 (141 ± 9) μm high and has one to four stalk cells and a thick transparent layer between the sporangial wall and spores.

Structure of oogonium Oogonial sori are scattered on both sides of the midrib and appear as a thin line or small spots with irregular outline (Fig. 8). The brownish color of oogonial sori is lighter than that of sporangial sori. An oogonial sorus consists of a large number of oogonia, which are at usually at the same developmental stage (Fig. 9). The oogonial formation begins by outward swelling of browned cortical cells. By further development, the oogonia, which are spherical to elliptical in shape, produce only one stalk cell below and completely project above the cortex (Figs. 10, 11). The mature oogonia are 40–76 (58 ± 8) μm across and 60–102 (85 ± 9) μm high.



Figs. 12–15. Antheridia of *Dictyopteris latiuscula*. Fig. 12. Surface view of a male gametophyte. Whitish antheridial sori are seen on both sides of a midrib. Fig. 13. Surface view of an antheridial sorus. Antheridia are tightly packed in a sorus. Fig. 14. Antheridial sori (TS) are formed both sides of a blade and project above the cortex. Fig. 15. Antheridia (TS). Each has a stalk cell at the base.

Structure of antheridium Antheridial sori appear whitish patches or belts along the midrib to the naked eyes (Fig. 12). In the initial developmental stage of sori, all of cortical cells that are in some elliptical or rectangular areas on the wing are transformed into antheridia (Figs. 13, 14). As maturation progresses, the sori expand by formation of new antheridia around. Consequently, union of neighboring sori producing larger sori occurs. The antheridia are quadratic prism in shape, 14–28 (20 ± 3) µm across and 46–76 (63 ± 6) µm high, projects above cortex and contains 13–24 layers in which 4–8 cubic loculi are arranged transversely (Fig. 15). The heights of antheridia are about the same level with neighbors. One or two stalk cells, 10–26 (16 ± 3) µm high, are divided below during the developing process of an antheridium.

Reproductive seasonality On yearly collection at Shimoda, *Dictyopteris latiuscula* was collected between in Apr. 22 and Oct. 28 in 2000 and then was not found until Apr. 11, 2001. Reproductive plants were collected between Jun. 20 (early summer) and Sep. 14 (early autumn). The sporophytes were found Jun. 20, Jul. 17 and Aug. 30. The female gametophytes were found only in Sep. 14. The male gametophyte was never found.

Discussion

The sporangial structures of *Dictyopteris latiuscula* observed in this study agree with Okamura (1907) in the features of sori and Kawai (2001) in those of sporangia. Female gametophyte and oogonial structure were reported for the first time in this study.

Among species of *Dictyopteris*, differences of sporangial and/or oogonial structures exist; either aggregated in sori or solitary, and either project above or embedded in the cortex. *Dictyopteris plagiogramma* (Montagne) Vickers (Phillips 2000), *Dictyopteris punctata* Noda (Hasegawa and Tanaka 2005), *Dictyopteris repens* (Okamura) Børgesen (Phillips 2000) and *Dictyopteris secundispiralis* J. A. Phillips (2000) produce solitary sporangia. *Dictyopteris gracilis* Womersley (Phillips 2000), *Dictyopteris muelleri* (Sonder) Reinbold (Phillips 2000), *Dictyopteris serrata* (Areschoug) Hoyt (Phillips 2000) and *Dictyopteris woodwardia* (R. Brown ex Turner) C. Agardh (Phillips 2000) produce solitary and embedded sporangia. Phillips (2000) suggested five patterns of sporangial distribution as 1) scattered in two elongate bands either side of and parallel to the midrib; 2) clustered around the reflexed hair bundles; 3) densely scattered within broad fertile zones which extend across the blade between the midrib and the sterile margin; 4) sparsely scattered down the mid blade; 5) in circular patches on the blade, and three patterns of oogonial distribution as 1) in elongate bands either side and parallel to the midrib; 2) scattered on the midblade; 3) densely scattered across the blade leaving the midrib and narrow marginal region sterile. Hasegawa and Tanaka (2000) reported additional distributional patterns of sporangia and oogonia in which both reproductive organs are densely produced in sori based on observation of *Dictyopteris prolifera* (Okamura) Okamura from Japan.

The sporangia and oogonia of *D. latiuscula* are both densely produced, form sori around the midrib and completely project above the cortex. As in the other species of *Dictyopteris*, antheridia of *D. latiuscula* densely produced around the midrib to form sori and project above the cortex. The reproductive features of *D. latiuscula* well accord with those of *D. prolifera* (Hasegawa and Tanaka 2000). Both species produce similar sporangial and oogonial sori in which reproductive organs are densely produced. Sporangia produce 1 to 4 stalk cells, and oogonia have only one stalk cell. The oogonia within a sorus develop synchronously in each species, although the sporangia at different developmental stage occur in a sorus. This should be the feature of oogonial formation of these two species and enables to distinguish oogonia from sporangia.

Dictyopteris latiuscula and *D. prolifera* also show similarity in those thallus structures constructed by successive proliferation. They are apparently different from the other species of *Dictyopteris* which mainly grow by dichotomy. These two species, endemic to Japan and adjacent regions, also coincide in reproductive structures.

Okamura (1907) described that sporangial sori of *D. latiuscula* are produced in spring, and no report has been made on reproductive seasonality ever since. We checked cast-up plants at Shimoda year-round between April 2000 and April 2001. Mature sporophytes were collected in summer. Mature gametophytes were collected only in early autumn and never with sporophytes, in 2000. In 1999, we collected sporophytes and male and female gametophytes at the same time (late in June and early in July) and the same location. At Ohara and Tateyama, Chiba Pref., mature sporophytes and female gametophytes were also collected together in late spring. Therefore, they are presumed to mature simultaneously.

The reproductive season of *D. latiuscula* seems to differ in each locality, and that of two sites in Chiba Pref. (spring) agree with Okamura (1907). As compared with annual seawater temperature data of Shimoda in 2000 (Shizuoka prefectural fisheries experimental station, Izu branch, 2001), the season that mature plants of *D. latiuscula* were collected was June, when the seawater temperature exceeded 20°C. Furthermore, in late

June and early July in 1999, when mature sporophytes and female and male gametophytes were collected, the seawater temperature of Shimoda exceeded 20°C. Thus, reproductive organ formation of *D. latiuscula* is estimated to start before the seawater temperature attains 20°C. For clarifying the definite temperature condition that the formation of reproductive organs of *D. latiuscula*, closer inspections of indoor cultures are needed.

The life history of *D. latiuscula* growing around Shimoda is assumed as follows; 1) annual, 2) plants attains dozens of centimeters in spring, 3) reproduction starts in early summer and continues until autumn, 4) in autumn, most blades are lost leaving hairy lower portion, then withered and dead, 5) sporelings slowly grow in lower seawater temperature season between winter and spring. To elucidate the exact life history of *D. latiuscula* in nature, we intend to discover a population of the species and to make continuative observation.

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長谷川和清，田中次郎：**日本太平洋沿岸産ヤハズグサ（褐藻，アミジグサ目）の生殖器官の形態と季節性**

本州関東地方太平洋沿岸よりヤハズグサを採集し，生殖器官の形態を観察した．雌性配偶体および生卵器は初報告である．すべての生殖器官は葉の翼部皮層上に突出する．胞子嚢は，楕円体から倒卵形で，1～4個の柄細胞を持ち，中肋に沿う斑状から帯状の胞子嚢群内に密集し，様々な発達段階のものが混在する．生卵器は，楕円体から倒卵形で，胞子嚢よりも小さく，柄細胞を1個持つ．密集して斑状から帯状の生卵器群を中肋周辺に成し，1群内での生卵器の発達は同調的である．造精器は，角柱形で，柄細胞を1～2個持つ．翼部のある範囲にある皮層細胞全てが一斉に造精器に分化し，中肋の両側に斑状から帯状の群を形成する。静岡県下田市における同種の成熟の季節性の一年間にわたる調査では，生殖器官を形成した胞子体と配偶体は，初夏から初秋にかけて採集された．生殖を行う時期は生育地間で異なり，胞子体と配偶体は同時に生育することが明らかになった．

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